THE GALIUM ANGUSTIFOLIUM COMPLEX (RUBIACEAE) OF CALIFORNIA AND BAJA CALIFORNIA

LAURAMAY T. DEMPSTER AND G. LEDYARD STEBBINS
Department of Botany, University of California, Berkeley 94720
Department of Genetics, University of California, Davis 95616

INTRODUCTION

There are three groups of dioecious *Galium* species endemic to western North America, of which the *G. angustifolium* complex is the smallest, both in number of species and in its range. The other two were treated in earlier papers, as follows: the *G. multiflorum* complex of western United States, Sonora and Baja California (Ehrendorfer, 1956; 1961; Dempster, 1959; Dempster and Ehrendorfer, 1965); the fleshy-fruited polyploid complex of California, Oregon and Baja California (Dempster, 1958; 1962; Dempster and Stebbins, 1965; 1968). The imperfectly dioecious, or polygamous, group exemplified by *G. parishii* Hilend & Howell and *G. wrightii* Gray has not been comprehensively dealt with, although its relationship to the *G. multiflorum* group is obviously close and, quite likely, ancestral.

All four groups have four-leaved whorls, with the exception of *G. hardhamae* Demp. of the fleshy-fruited group, which has six leaves per whorl. The *G. angustifolium* complex, subject to the present paper, has important characters in common with the *G. multiflorum* group and the polygamous *G. parishii* group, notably the long straight specialized fruit hairs and the three-nerved leaves. Resemblance to the fleshy-fruited group is less marked, but is apparent in the rather extraordinary habit of reaching upward with greatly elongated stems which later become the slender woody scaffolds for subsequent herbaceous growth. Much of *G. angustifolium* Nutt. of the present group, and especially *G. nuttallii* Gray of the fleshy-fruited group exemplify this character.

The distribution of the present group, unlike that of the *G. multiflorum* complex, is not archipelagic, but resembles more that of the fleshy-fruited group in that it is largely continuous. Its occurrence (fig. 1) is chiefly in the southern coastal ranges, from the Sierra San Pedro Mártir of Baja California, northward into the Santa Lucia and Gabilan ranges of Monterey and San Benito counties. In Kern Co. it also occurs farther inland in the Tehachapi, Greenhorn, and Piute ranges, and at the southern end of the Sierra Nevada west of the crest. In the Mohave Desert it has been collected as far east as the Providence Mountains.

The *G. angustifolium* complex consists of one narrowly endemic, diploid, uniform species, *G. jepsonii*, one widely distributed polymorphic species on three ploidy levels, *G. angustifolium*, and one local hexaploid species, *G. johnstonii*, which apparently originated by hybridization from the other two. *Galium johnstonii* expresses its hybrid origin in

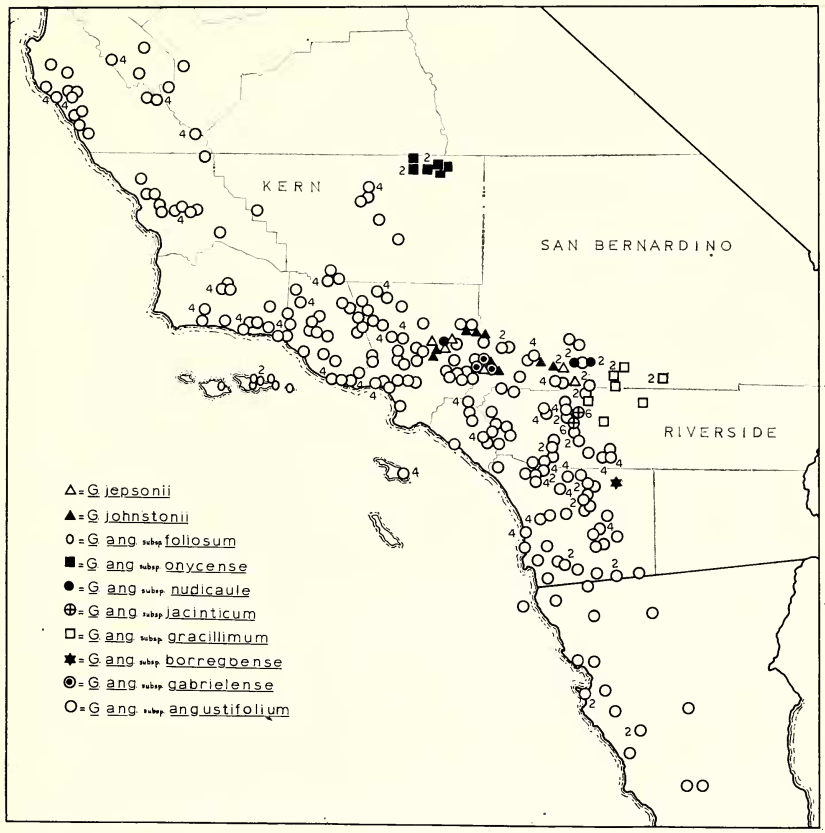

FIG. 1. Map showing entire distribution of the *G. angustifolium* complex. Numbers indicate actual chromosome counts divided by 11.

great variability within small populations, but seems to be genetically isolated from both parental species and is not taxonomically subdivisible. *Galium angustifolium*, on the other hand, is divisible into subspecies, of which the number recognized is limited chiefly by practical considerations. Unfortunately the diploids are not clearly separated from the tetraploids with respect to morphology and geography. Consequently we must content ourselves with describing as separate subspecies several of the forms which are morphologically uniform and geographically restricted, leaving the large remainder, both diploid and tetraploid, under ssp. *angustifolium*. Throughout this paper, all subspecies mentioned should be understood as belonging to *G. angustifolium*.

Were it not for the existence of the intermediate species *G. johnstonii*, there would scarcely be adequate reason to include *G. jepsonii* in the *G. angustifolium* complex. The concentration of leaves near the base of the plant, the truly campanulate corollas, and the short falcate ovary- and fruit-hairs all set *G. jepsonii* sharply apart. There is furthermore

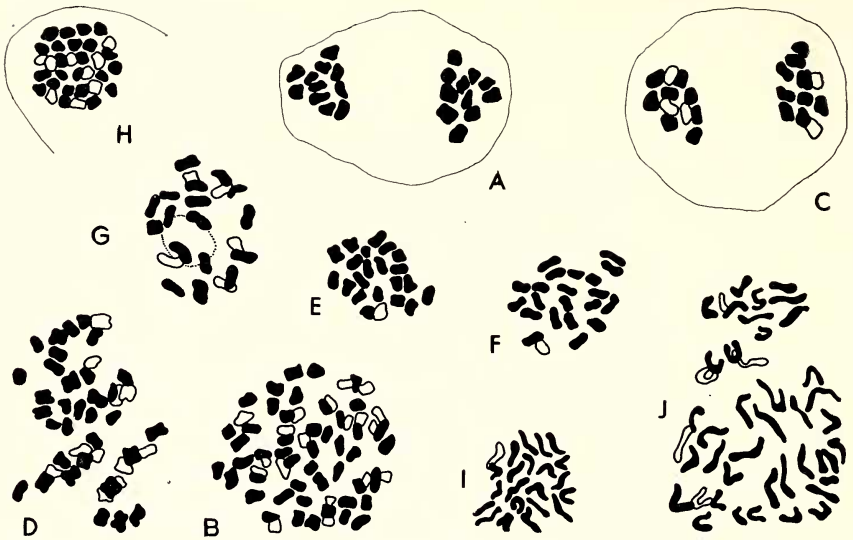

FIG. 2. Representative chromosome figures × 1700: A, *G. jepsonii,* meiotic, **n = 11** *(4120);* B, *G. johnstonii,* mitotic, **2n = 66** *(4118);* C-J, *G. angustifolium;* C, ssp. *angustifolium,* meiotic, **n = 11** *(4128);* D, ssp. *angustifolium,* mitotic, **2n = 44** *(4067);* E, ssp. *foliosum,* mitotic, **2n = 22** *(4083);* F, ssp. *onycense,* mitotic, **2n = 22** *(4207);* G, ssp. *gracillimum,* mitotic, **2n = 22** *(4174);* H, ssp. *jacinticum,* meiotic, 1 pole, **n = 33** *(4129);* I, ssp. *nudicaule,* mitotic, **2n = 22** *(4147);* J, ssp. *gabrielense,* mitotic, **2n = 44** *(4295).*

no evidence that genes from *G. jepsonii* are present in any subspecies of *G. angustifolium,* nor that hybridization between the two species ever occurs on the diploid level. It is possible that *G. johnstonii* originated only once, perhaps from unreduced gametes of *G. jepsonii* and tetraploid *G. angustifolium.*

Any definition of the complex is therefore brief: plants perennial, dioecious, with 4 leaves to a node (i.e., 2 leaves and 2 stipular appendages, looking exactly alike); the generally narrow leaves obscurely 3-nerved, the marginal hairs spreading or apically directed; fruits with specialized hairs which are not uncinate.

The present group has gone a little farther with polyploidy than has the *G. multiflorum* complex, although not nearly so far as the fleshy-fruited group (Dempster and Stebbins, 1965; 1968). Of the species and subspecies here recognized, 5 are diploid, 1 tetraploid, 1 indistinguishably diploid and tetraploid, 2 hexaploid, and 1 unknown (fig. 2, table 1). The basic chromosome number is 11. The geographically isolated subspecies *foliosum* and *onycense* are both diploid. No comparable degree of isolation occurs within the fleshy-fruited group, although it is usual in the *G. multiflorum* complex.

The center of evolutionary activity appears to have been in the San Gabriel, San Bernardino, and San Jacinto Mountains, where the great

TABLE 1. CHROMOSOME COUNTS IN THE GALIUM ANGUSTIFOLIUM COMPLEX

(An asterisk after a collection number means that the count was about the number reported. All counts are from California, except the first two listed.)

G. angustifolium ssp. *angustifolium*. **2n = 22.** Baja California. Santo Tomas, *4229;* Punto Banda, *Hardham & Dempster 17,010**. Riverside Co.: *1890**; *4128*; *4131; 4134; 4177; 4178; 4239; 4241; 4245.* San Bernardino Co.: *4126; 4145**; *4149**. San Diego Co.: *4179; 4181*;4182**; *4183; 4330; Bacigalupi 8282; Bacagalupi 8288; Bacigalupi 8371**. **2n = 44.** Kern Co.: *4208**; *4218.* Los Angeles Co.: *4114**; *4115**; *4116*; *4117*; *4169**; *4172**; *4190; 4191**; *4216; 4369**; *4731.* Monterey Co.: *4067*; *4159; 4161**; *4193.* Orange Co.: *4352**; *4354**. Riverside Co.: *4137**; *4176**; *4249; 4258; 4276.* San Benito Co.: *4194**. San Bernardino Co.: *4141**; *4142; 4152; 4154**. San Diego Co.: *4189**; *4333; 4336**; *4340**; *4341**; *4347**; *Hardham & Dempster 17,013.* San Luis Obispo Co.: *Stebbins* s. n.*. Santa Barbara Co.: *4163**; *4164**; *4166**; *4167.* Ventura Co.: *4111; 4113**; *4168**.

G. angustifolium ssp. *foliosum*. **2n = 22.** Santa Barbara Co.: *4083.*

G. angustifolium ssp. *gabrielense*. **2n = 44.** Los Angeles Co.: *4295.* San Bernardino Co.: *4294**.

G. angustifolium ssp. *gracillimum*. **2n = 22.** San Bernardino Co.: *4173; 4174.*

G. angustifolium ssp. *jacinticum*. **2n = 66.** Riverside Co.: *4129; 4130; 4244**; *4246**.

G. angustifolium ssp. *nudicaule*. **2n = 22.** Los Angeles Co.: *4123**; *4236.* San Bernardino Co.: *4147; 4150.*

G. angustifolium ssp. *onycense*. **2n = 22.** Kern Co.: *4206**; *4207.*

G. jepsonii. **2n = 22.** Los Angeles Co.: *4120; 4122.* San Bernardino Co.: *4143.*

G. johnstonii. **2n = 66.** Los Angeles Co.: *4118, 4121.*

majority of forms are to be found (fig. 3). Tetraploidy probably occurred repeatedly, involving ssp. *nudicaule* at least once to produce ssp. *gabrielense,* and perhaps once again in the production ultimately of hexaploid ssp. *jacinticum*. Other tetraploids, probably not involving either *G. jepsonii* or ssp. *nudicaule,* produced the taller forms of ssp. *angustifolium* which spread northward and westward, remaining regionally sympatric with the diploid form in San Diego Co. and the San Jacinto and San Bernardino Mountains, and occupying alone the northern and western remainder of the range, including the lower altitudes of the San Gabriel Mountains. The desert diploid ssp. *gracillimum* probably originated from the tall southern diploid by selection for the desert habitat. Subspecies *onycense,* on the other hand, is probably much more ancient in its isolation, and had not obviously contributed to any polyploid. The diploid island race ssp. *foliosum* is probably also very ancient, and may or may not have been involved in the production of the mainland tetraploids.

Again, in this group, for the third time, we find hispid polyploids with no visible hispid diploid progenitors. In the *G. multiflorum* complex (Dempster and Ehrendorfer, 1965) we observed two very hispid tetraploids, *G. hilendiae* Dempster & Ehrend. and *G. munzii* Hilend & Howell, the former related to diploid *G. multiflorum* Kell. and the latter to diploid *G. magnifolium* Dempster, both lacking any obvious, adequately hispid diploid ancestor. In the fleshy-fruited group (Dempster

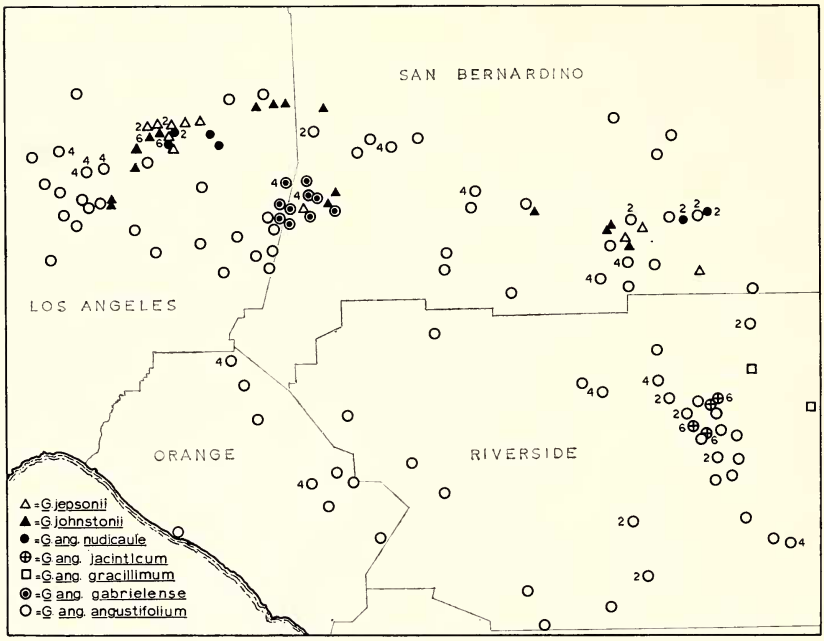

FIG. 3. Map showing distribution in greater detail, particularly in the San Gabriel, San Bernardino, and San Jacinto mountains. Numbers indicate actual chromosome counts divided by 11.

and Stebbins, 1965; 1968), the hispidity of some of *G. bolanderi* Gray and *G. andrewsii* Gray ssp. *gatense* (Dempster) Dempster & Stebbins cannot be adequately explained by assuming hybridization between existing diploids. In the present group, the hispid tetraploid forms of ssp. *angustifolium,* as well as the hispid tetraploid ssp. *gabrielense,* cannot be explained with reference to existing diploids. One may postulate the extinction of one hairy diploid ancestor, but it strains credulity to suppose that only the hairy diploids have become extinct in all three of our dioecious West American species groups. One is left to wonder whether some additive genetic mechanism may not be at work to cause greater hairiness in some polyploids than was expressed in their diploid ancestors.

MORPHOLOGY

Habit is of some taxonomic importance. Low tufted forms, lacking woody stems above ground (fig. 4A-C), characterize *G. jepsonii,* ssp. *nudicaule,* usually ssp. *gabrielense,* and sometimes ssp. *angustifolium.* Taller forms with perennial scaffold stems (fig. 4D), as in much of ssp. *angustifolium,* may grow as high as 100 cm.

Stems in this genus are 4-sided, i.e., basically square in cross section. The angles are, however, more or less thickened and broadened by ex-

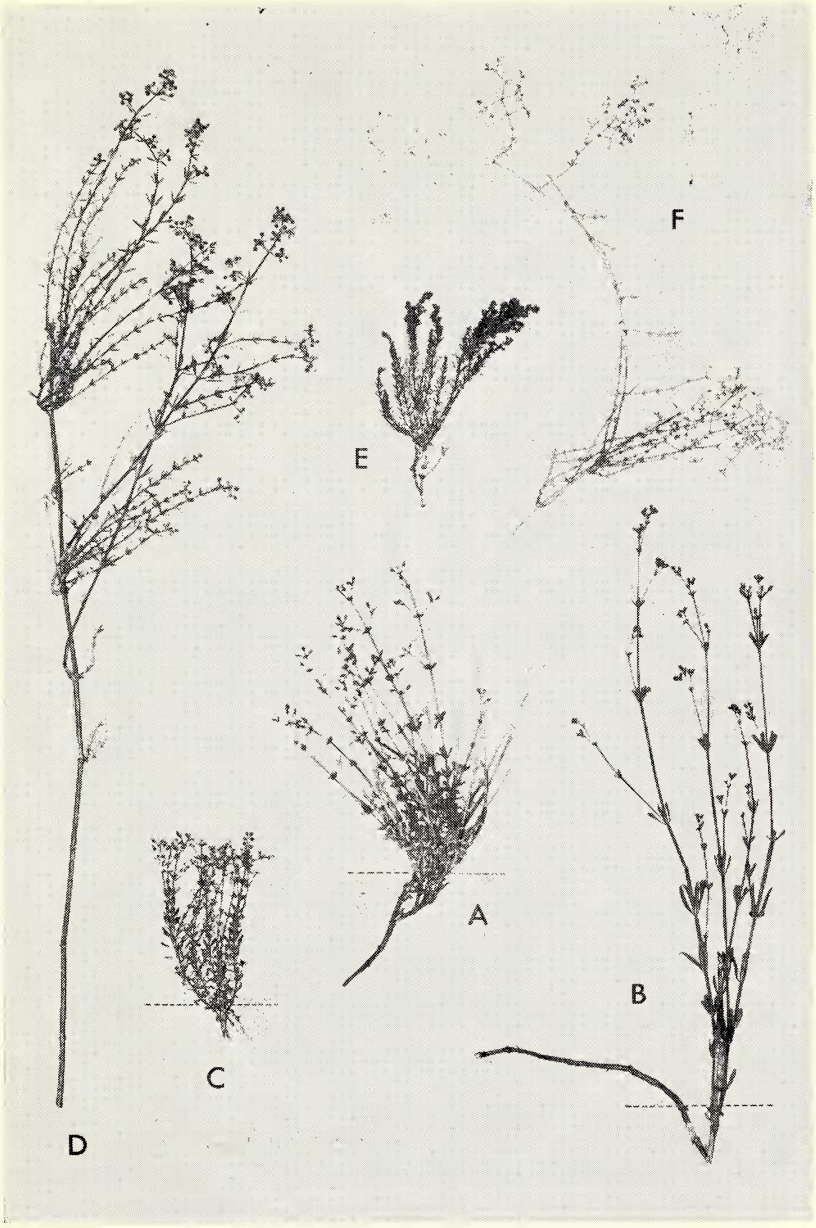

FIG. 4 Some representative habits × ⅓. In A, B, and C, ground level is indicated by dotted lines; D, E, and F are fragments broken off well above ground level. A, *G. jepsonii,* Cloudburst Summit *(4235);* B, *G. johnstonii,* Chilao Recreation Area *(4234);* C-F, *G. angustifolium:* C, ssp. *nudicaule,* Cloudburst Summit *(4236);* D, ssp. *angustifolium,* Little Thomas Mountain *(4347);* E, ssp. *foliosum,* Santa Rosa Island *(Niehaus 459);* F, ssp. *gracillimum,* 49 Palms Canyon *(4174).*

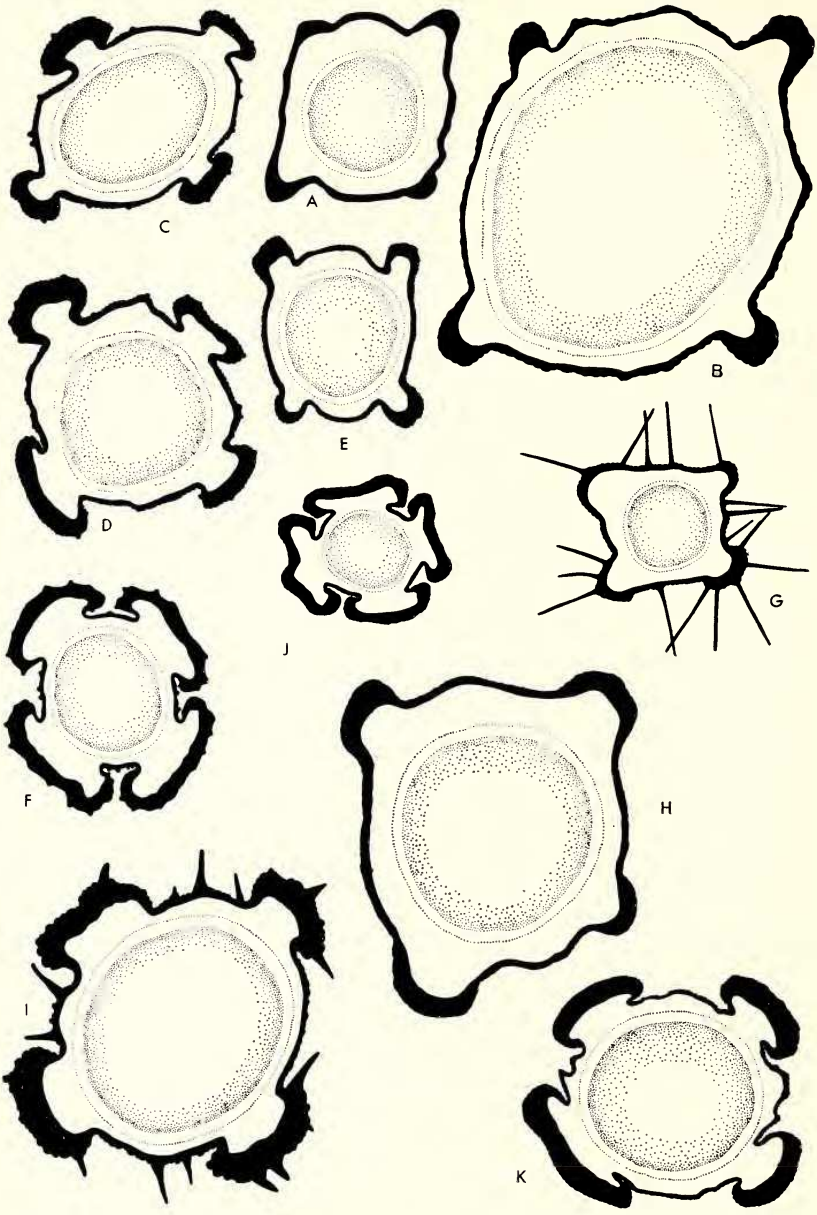

FIG. 5. Stem cross sections, × 24, to show comparative development of the angles. Collenchyma tissue with epidermis shown in black; stippled areas represent xylem, dotted circles endodermis. Size differences, although partially dependent on age of stems, are nonetheless of some taxonomic importance. A, *G. jepsonii,* San Gabriel Mountains *(4235);* B, *G. johnstonii* north side San Gabriel Mountains *(4156);* C-K, *G. angustifolium;* C, ssp. *nudicaule,* San Bernardino Mountains *(4147);* D, ssp.

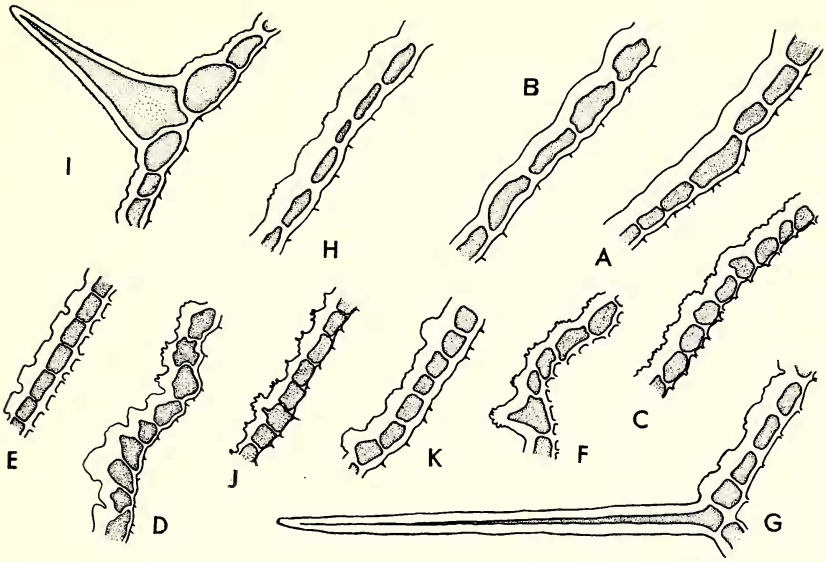

FIG. 6. Details of epidermis from the sides (not angles) of the stem cross sections in FIG. 5: A, *G. jepsonii;* B, *G. johnstonii;* C-K, *G. angustifolium:* C, ssp. *nudicaule;* D, ssp. *gracillimum;* E, I, ssp. *angustifolium;* F, ssp. *onycense;* G, ssp. *gabrielense;* H, ssp. *jacinticum;* J, ssp. *borregoense;* K, ssp. *foliosum.* All × 140.

trusion of the cortex and addition of collenchyma. Such enlargement of the angles occurs in varying degrees in the different species and subspecies of this group (fig. 5). It is least developed in *G. jepsonii* (fig. 5A), and has been carried to such an extreme in young stems of ssp. *borregoense* (fig. 5J) and ssp. *onycense* (fig. 5F) that the angles appear as sides and the nearly covered sides appear as mere longitudinal fissures. Subsequent growth in width of the stems causes the sides to emerge into visibility.

Stems are chiefly glabrous, but in ssp. *gabrielense* (fig. 5G) and in much of the tetraploid material of ssp. *angustifolium* (fig. 5I) they are well supplied with hairs. Stems of ssp. *nudicaule* (fig. 5C), and others to a less noticeable degree, are papillose, the papillae consisting of solitary enlarged epidermal cells. Figure 6 shows details of the epidermis of the sides (not angles) of the stems illustrated in fig. 5.

All plants of the *G. angustifolium* complex apparently have stomata on both leaf surfaces. All leaves have 3 nerves, although the 3-nerved condition is not very obvious, and the lateral nerves, even when seen in

gracillimum, Black Rock Spring (*Cole 989,* POM); E, ssp. *angustifolium,* diploid form from Rincon Springs, San Diego Co. *(4339);* F, ssp. *onycense,* east of Onyx *(1432);* G, ssp. *gabrielense,* Ontario Peak *(Johnston 1616,* UC); H, ssp. *jacinticum* (*4244,* type); I, ssp. *angustifolium,* hairy tetraploid form from Del Mar *(4347);* J, ssp. *borregoense,* Palm Canyon *(4375);* K, ssp. *foliosum,* Santa Cruz Island *(Ellison s.n.,* UC).

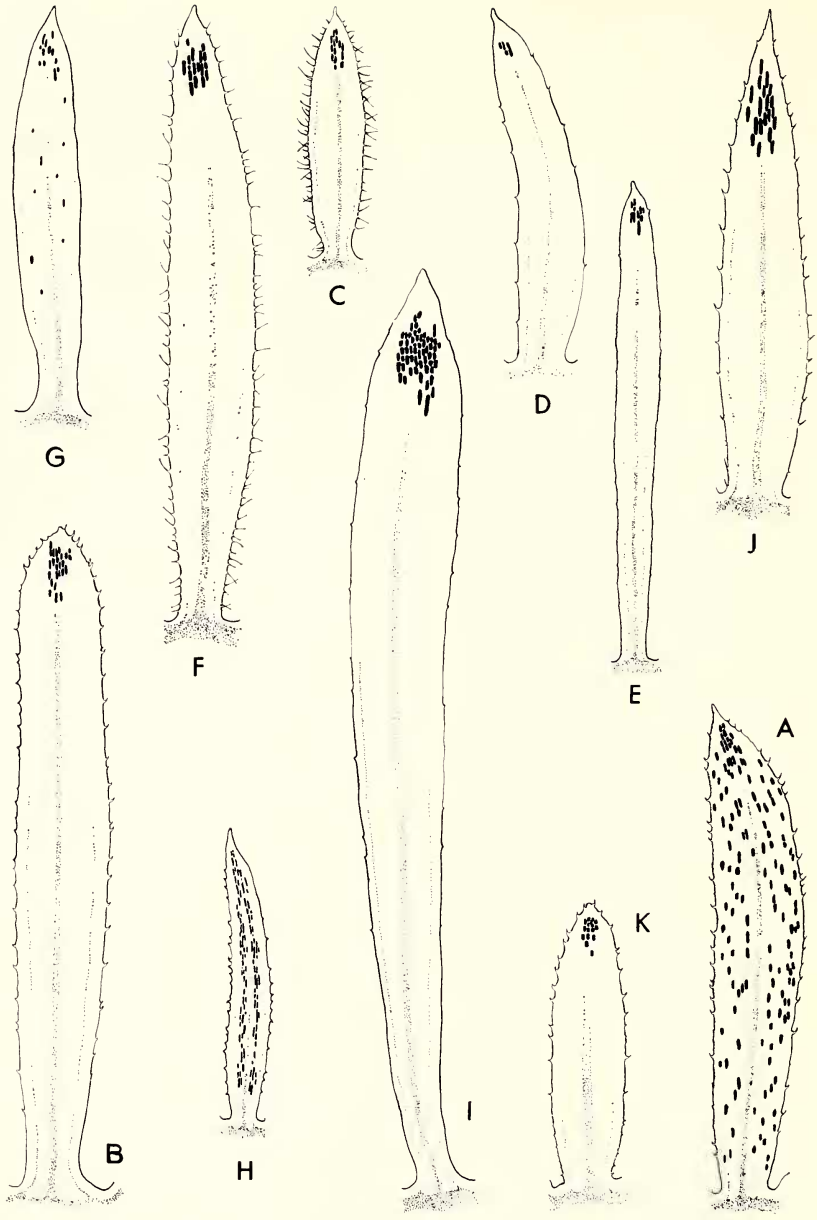

FIG. 7. Leaves × 7, cleared and stained to show principal veins, distribution of secretory cells, and features of the leaf margins. All surface hairs have been omitted. A, *G. jepsonii,* Cloudburst Summit *(4235);* B, *G. johnstonii,* Chilao Recreation Area *(4234);* C-K, *G. angustifolium;* C, ssp. *gabrielense,* San Antonio Mountains (*Raven 11,232,* CAS, JEPS); D, ssp. *foliosum,* Anacapa Island (*Hoffmann s.n.,* CAS); E, ssp. *angustifolium,* Catalina Island (*Fosberg S4354,* SMU, UC); F, ssp.

cleared and stained leaves, are sometimes tenuous, or even interrupted in very small leaves, as in ssp. *foliosum*.

Leaves (fig. 7), except the lowest, are for the most part strapshaped. Surface hairs are usual, and at least a few marginal hairs are nearly always present. Hairs vary considerably in length and stoutness, but are always either spreading or apically directed (fig. 9), never basally directed as in some members of the fleshy-fruited group.

The presence and distribution of secretory cells on the under side of the leaves is an important taxonomic character. These cells, of unknown function, have been observed in *Galium* species having 4-leaved whorls both in Europe (Nicolas, 1929) and in North America (Dempster and Ehrendorfer, 1965; Dempster and Stebbins, 1968). They are most commonly found clustered just below the leaf apex (fig. 7B-G, I-K) but are sometimes distributed over the entire lower surface, as in *G. jepsonii* (fig. 7A) and sometimes ssp. *angustifolium*. In ssp. *gracillimum* (fig. 7H) they occur in 2 bands at either side of the midrib. Table 2 summarizes our observations of this feature in the *G. angustifolium* complex, and shows that there is a considerable degree of taxonomic consistency with respect to this character.

Corollas of *G. angustifolium* are in general rotate, in conformity with the Linnaean description of the genus (fig. 8C-J). Old corollas especially, however, may be a little cupped at the base, so that they need to be cut before they will lie flat. The occurrence of truly campanulate corollas in *G. jepsonii* (fig. 8A) and its derivative *G. johnstonii* (fig. 8B) adds another to an increasing list of *Galium* species known to have this contra-diagnostic character (see discussion, Dempster and Ehrendorfer, 1965; Dempster, 1968).

The occurrence of hispid corollas in conjunction with glabrous or relatively glabrous herbage is also of interest. This character occurs not only in the present group, but also in the *G. multiflorum* complex, where it is diagnostic of the two species *G. matthewsii* Gray and *G. magnifolium* Dempster. It is apparent that hispid corollas may be produced in either of two ways: 1, by genes for general hairiness, the commoner situation, wherein the corolla hairs are commensurate in size and abundance with those on stems and leaves; and 2, by a separate gene or genes, as in *G. angustifolum* ssp. *nudicaule* (fig. 8F), *onycense* (fig. 8D), *gabrielense* (fig. 8H), *borregoense* (fig. 8G) and *jacinticum* (fig. 8J). In the latter circumstance, the corolla hairs are usually long, stout, abundant, and conspicuous, often quite disproportionately to those, if any, on stems and leaves. Since hairs occur only on the outside of the corollas, they are especially noticeable before the buds open. This character is apparent even to the naked eye, and is therefore very useful

angustifolium, Castle Peak *(4067);* G, ssp. *borregoense,* Palm Canyon *(4375);* H, ssp. *gracillimum,* type locality (*Cole 989,* POM); I, ssp. *jacinticum,* Fulmor Lake *(4129);* J, ssp. *onycense,* Spanish Needle Creek (*Twisselmann 10,911,* CAS, JEPS); K, ssp. *nudicaule,* Cloudburst Summit *(4236).*

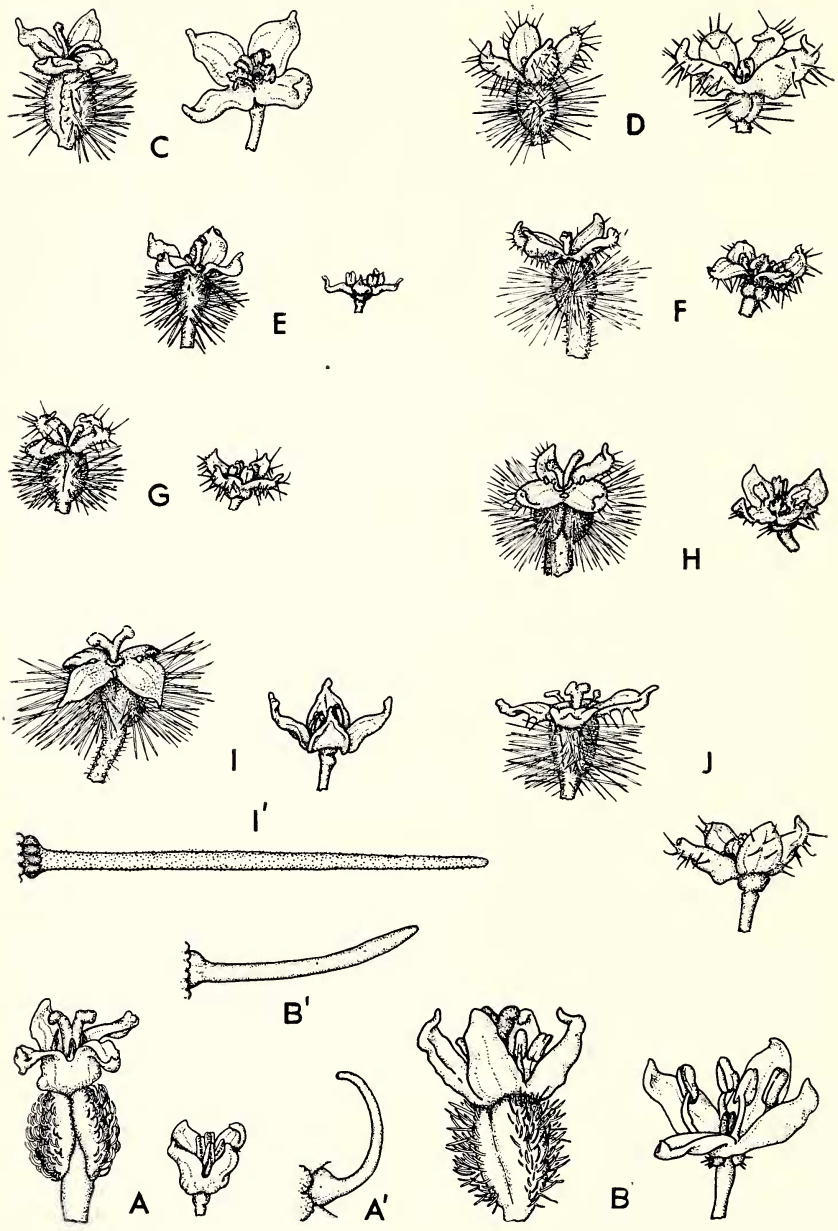

FIG. 8. Pistillate and staminate flowers, × 6: A, *G. jepsonii,* Cloudburst Summit *(4235).* B, *G. johnstonii,* Big Pines *(4156).* C-J, *G. angustifolium:* C, ssp. *foliosum,*

Table 2. Distribution of Secretory Cells on the Lower Surface of the Leaves (fig. 7)

Taxon	Number of individuals with secretory cells			
	clustered below leaf apex (subapical)	subapical plus a few scattered	mostly scattered over entire surface	none seen
G. angustifolium				
ssp. *angustifolium*	15	8	11	13
ssp. *borregoense*	1	1		
ssp. *foliosum*	5 (few)			4
ssp. *gabrielense*	6			2
ssp. *gracillimum*			9 (2 ranks)	1
ssp. *jacinticum*	2	2		1
ssp. *nudicaule*	3	1		1
ssp. *onycense*	5			5
G. jepsonii			7	
G. johnstonii	8			

in identification. Its presence also provides a valuable clue to the origin of the polyploid sspp. *gabrielense* and *jacinticum*.

All races and subspecies of *G. angustifolium,* like all members of the *G. multiflorum* complex and of the polygamous *G. parishii* group, are characterized by long straight spreading hairs on ovaries and fruits (fig. 8I'). *Galium jepsonii,* however, has short, upwardly curved hairs (fig. 8A'), and those of *G. johnstonii* are variably intermediate with respect to both length and curvature (fig. 8B').

Acknowledgments

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Material from the following herbaria was examined, annotated, and most will not be cited: CAS, JEPS, NO, POM, RSA, SBBG, SBM, SMU, UC, UCSB. All unassigned numbers in this paper refer to collections (JEPS) of Dempster or of Dempster and Stebbins.

Anacapa Island (*Howell 3792,* CAS, POM); D, ssp. *onycense,* Spanish Needle Creek (*Twisselmann 10,924, 10,911,* CAS, JEPS); E. ssp. *gracillimum,* Snow Creek Canyon (*Wolf 3648,* RSA, UC), Black Rock Spring (*Cole 990,* POM); F, ssp. *nudicaule,* Cloudburst Summit *(4236);* G, ssp. *borregoense,* Palm Canyon (*Munz & Hitchcock 11,339,* POM, *Dempster 4375*); H, ssp. *gabrielense,* Sunset Trail, *Johnston s.n.,* POM), San Antonio Canyon (*Roos 400,* POM); I, ssp. *angustifolium,* Del Mar *(4347),* Sespe Creek *(4111);* J, ssp. *jacinticum* (type, *4244*). Position of corolla lobes depends considerably on the developmental stage. Size of corollas, although it varies with the individual, is nevertheless significant taxonomically. A', B', I', ovary hairs × 40, to show relative size, shape and position: A', *G. jepsonii;* B', *G. johnstonii;* I', *G. angustifolium.*

KEY TO THE SPECIES AND SUBSPECIES

Fruiting pedicels 1–4 times as long as fruits; upper nodes much longer than the lower, the leaves often congested toward base of plant; fruits appearing longer than wide, the hairs shorter than the fruit body; corollas usually more or less cupped or campanulate.
- Plants low, generally less than 16 cm high; corollas cleft about halfway, the lobes little spreading; secretory cells evenly distributed; diploid *G. jepsonii*
- Plants tall, generally over 18 cm high; corollas deeply cleft, spreading; secretory cells subapical; hexaploid . . . . . *G. johnstonii*

Fruiting pedicels usually shorter than fruits; nodes approximately equal, the leaves not congested toward base of plant; fruits, with hairs, appearing spherical, the hairs usually as long as fruit body; corollas rotate . *G. angustifolium*
- Corollas usually hispid (not always in ssp. *jacinticum*).
  - Stems glabrous or nearly so.
    - Inflorescences narrow, relatively few-flowered, the branching little compounded.
      - Plants 6–16 cm high; leaves mostly 2–10 mm long; San Gabriel and San Bernardino mountains; diploid . . . . . ssp. *nudicaule*
      - Plants 17–35 cm high; leaves 11–26 mm long; San Jacinto Mountains; hexaploid . . . . . ssp. *jacinticum*
    - Inflorescences pyramidal, many-flowered, compoundly branched; plants 35–50 cm high; Borrego Desert . . . . . ssp. *borregoense*
  - Stems not glabrous.
    - Stems merely scabrous, the hairs few and shorter than those on the leaves; angles of stems much thickened, often nearly concealing the faces; northeastern Kern Co.; diploid . . . . . ssp. *onycense*
    - Stems hispid, the hairs usually abundant and long like those on the leaves; angles of stems narrow; vicinity of San Antonio Canyon, Los Angeles and San Bernardino counties; tetraploid . . . . . ssp. *gabrielense*
- Corollas usually glabrous, or not more hispid than stems and leaves.
  - Internodes of scaffold stems short, often shorter than the leaves; plants generally glabrous, the leaves very slender, often crowded; northern group of Channel Islands . . . . . ssp. *foliosum*
  - Internodes of scaffold stems long, generally much longer than the leaves, the leaves thus never crowded; not in northern Channel Islands.
    - Plants tall and very slender, essentially glabrous; flowers, fruits and leaves diminutive, the latter early deciduous; deserts, San Bernardino and Riverside counties . . . . . ssp. *gracillimum*
    - Plants stouter, tall or sometimes lower and tufted, glabrous to often canescent; flowers, fruits, and leaves larger, the latter not soon deciduous; widespread in hills and mountains, but not in the deserts. ssp. *angustifolium*

GALIUM JEPSONII Hilend & Howell, Leafl. W. Bot. 1:135. 1934. Based on *G. angustifolium* var. *subglabrum* Jepson, Manual Fl. Pl. Calif. 962. 1925. Type from Whitewater Basin, *Wilder 1113* (UC), undoubtedly from San Bernardino Co.

Plants low (fig. 4A), the erect glabrous stems commonly 8–16 cm high, arising in small clumps from widely spreading slender rhizomes or small woody base; leaves congested at the lower third or half of the stem, the upper portion having conspicuously elongated nodes and reduced leaves (fig. 4A), internodes of the lower, leafy portion ½ to as long as leaves, internodes of the upper portion 2–5 times as long as leaves; leaves 6–15

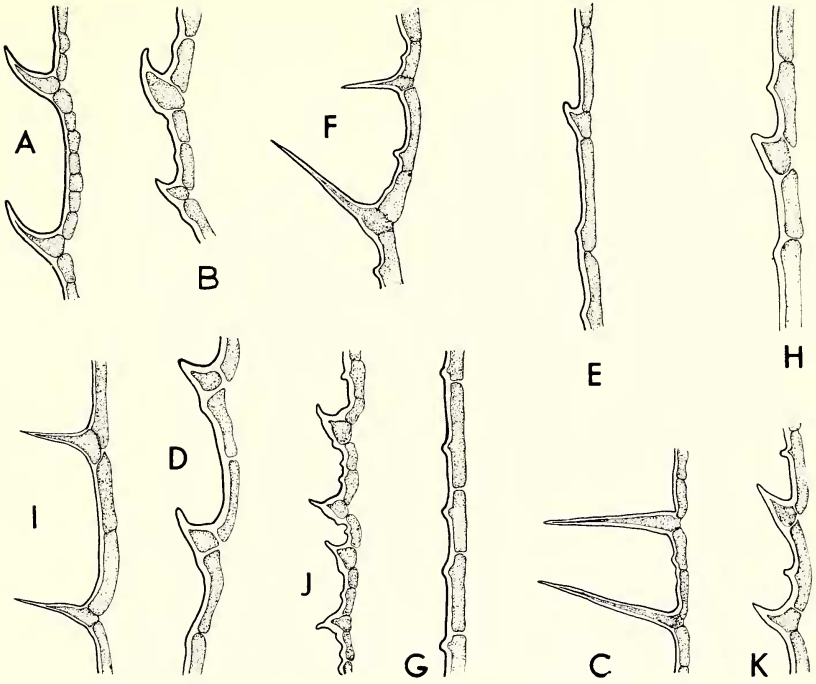

FIG. 9. Details of margins of the leaves in FIG. 7: A, *G. jepsonii;* B, *G. johnstonii;* C-K, *G. angustifolium;* C, ssp. *gabrielense;* D, ssp. *foliosum;* E, F, ssp. *angustifolium;* G, ssp. *borregoense;* H, ssp. *jacinticum;* I, ssp. *onycense;* J, ssp. *gracillimum;* K, ssp. *nudicaule.* All × 45.

mm long, thick, broadly linear, often a little falcate, the insertion broad, the apex narrowed rather suddenly to an obtuse, apiculate or sometimes acute, but not pungent, apex; leaf surfaces glabrous, the margins set with many short, rather stout, apically directed hairs; secretory cells scattered over the lower surface of the leaves; inflorescences lax, strict, relatively few-flowered, the short branches far apart, little compounded and strongly ascending; corollas glabrous, greenish, becoming cream-color and usually tipped with pink, campanulate, cleft about half-way, the tube somewhat fleshy, the lobes erect or scarcely spreading; ovaries of pistillate flowers not obviously hairy, but set with two tufts of ascending falcate hairs much shorter than the width of the ovary; fruits relatively few, the carpels 1¾ mm long, the upwardly curved hairs much shorter, the pedicels 1 to 4 times as long; **2n = 22.**

Openly wooded slopes, sandy granite soil, in mixed forest with *Pinus ponderosa.* San Gabriel and San Bernardino mountains, Los Angeles and San Bernardino counties, at 6400 to 7800 feet.

This heretofore little known and seldom collected diploid species is actually abundant at high elevations in the San Gabriel and San Bernardino mountains. Although inconspicuous and unprepossessing, it is un-

usual in several ways. Its relationship to *G. angustifolium* is apparent only by such general common characters as dioecy, 4-leaved whorls, 3-nerved leaves and dry fruits with specialized hairs. A fairly close relationship is further indicated by the highly probable assumption that the two species hybridized to produce *G. johnstonii*. *Galium jepsonii* has, however, certain extraordinary characters which distinguish it sharply from *G. angustifolium,* namely the fleshy campanulate corollas (fig. 8A), the short ascending falcate hairs of the ovaries and fruits (fig. 8A'), and the habit of sudden stem elongation above a congested leafy plant base. All of these characters, otherwise unique in the group, reappear commonly in individuals of the hexaploid *G. johnstonii* and nowhere else. The evenly distributed secretory cells are also diagnostic (fig. 7A), but this character also occurs sporadically in ssp. *angustifolium*.

Representative collections. Los Angeles Co.: San Gabriel Mountains, *Bacigalupi 6422* (JEPS), *Ewan 8415* (NO), *8438* (NO). San Bernardino Co.: San Antonio Mountains, *Johnston 6612* (CAS); San Bernardino Mountains, Jenks Lake, *4143*.

Galium johnstonii Dempster & Stebbins, nom. et stat. nov. Based on *G. angustifolium* var. *pinetorum* Munz & Johnston, Bull. Torrey Club 49:357. 1922. Type from Sierra Madre Mountains, Los Angeles Co., *Davidson* (UC). Not *G. pinetorum* Ehrend, Osterr. Akad. Wiss., Math.-Naturwiss, Kl., Sitzungsber., Abt. 1, Biol. 169:410. 1960.

Plants moderately tall (fig. 4B), the new shoots 18–38 cm high from a woody base, or sometimes arising from persistent woody stems up to 20 cm long; stems glabrous, the internodes generally longer than the leaves (except sometimes the lowest), the upper internodes often greatly elongated (2 to 5 times as long as leaves); leaves often somewhat thick, mostly narrowly linear, often a little falcate, 14–30 mm long, with broad insertion and obtuse or usually acute apex, the margins set with short, rather stout, apically directed hairs, the surfaces glabrous or set with minute curved hairs; secretory cells subapical; inflorescences very lax, few-flowered, racemosely or somewhat cymosely few-branched, the short branches ascending-divaricate; corollas relatively large, 3–5 mm across, glabrous, green, becoming pale yellow, rotate to flaring-campanulate with lobes much longer than tube; ovaries often longer than wide, set with few to many upward-curving or straight and spreading hairs, shorter than the length of the ovary, or sometimes as long; fruits relatively large, the body 2½–3 mm long, the hairs spreading, usually shorter than the body, the pedicels commonly 1–3 times as long. **2n = 66.**

In open mixed forest, on lightly shaded slopes, at 5100 to 7300 feet; granitic sand. San Gabriel and San Bernardino Mountains, Los Angeles and San Bernardino counties.

This hexaploid species is so clearly intermediate between ssp. *angustifolium* and *G. jepsonii* as to leave little doubt as to its hybrid origin (table 3; fig. 10). Although the altitudinal range of *G. johnstonii* is a

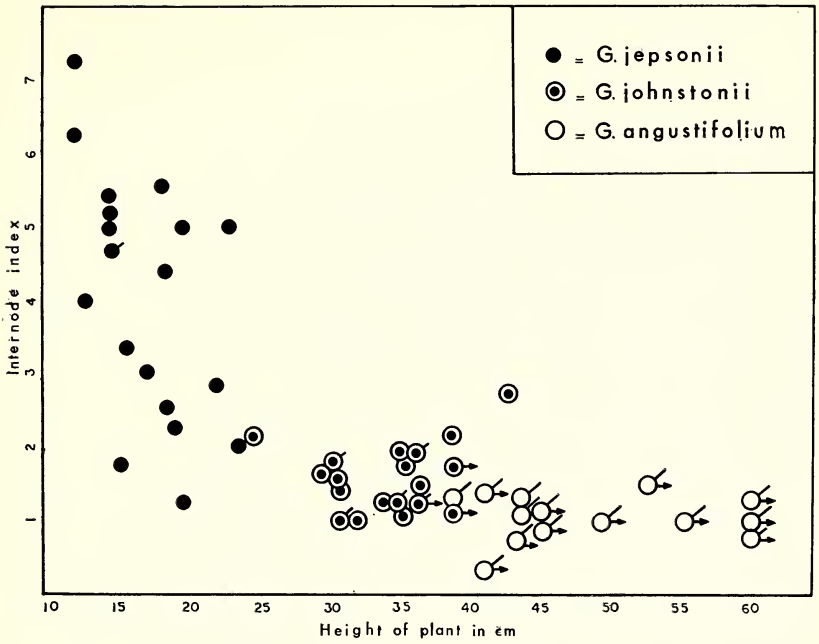

FIG. 10. Scatter diagram to show intermediacy of *G. johnstonii* between *G. jepsonii* and *G. angustifolium*. The internode index, derived from current year's shoots, was obtained by dividing the length of the internode ⅓ of the distance from the top, by the length of the internode ¼ of the distance from the bottom. A low figure indicates little difference, a high figure much difference. Arrow indicates that plant was taller than the measurement obtained. Long oblique line indicates ovarian hairs longer than ovary width, short line hairs about as long, no line hairs shorter than ovary width. All suitable pistillate plants were measured, from the San Gabriel Mountains only.

little lower than that of *G. jepsonii,* their ranges largely overlap, and the two species have been collected together twice by us (*4120* & *4121, 4233* & *4234*) and once by *Howe* (*45,584,* UC). We have not found either species growing with *G. angustifolium,* although they are regionally sympatric and their altitudinal ranges are not mutually exclusive.

Galium johnstonii is recognized first by its habit (fig. 4B), which is very lax, few-flowered, few-leaved and moderately low, and often demonstrates some gigantism in leaves, flowers and fruits. Closer examination will disclose the flaring campanulate corollas or, failing that, the short and often falcate ascending hairs of ovaries or fruits. The plants are too large to be confused with *G. jepsonii,* and the corollas much more like those of *G. angustifolium.* A solitary staminate individual may sometimes be mistaken for *G. angustifolium,* but pistillate individuals are unmistakable by virtue of their long pedicals and the short hairs on ovaries or fruits (fig. 8B').

Table 3. Some Comparisons, Showing Intermediate Position of Galium johnstonii between G. jepsonii and G. angustifolium ssp. angustifolium in the Same General Area

jepsonii	*johnstonii*	*angustifolium*
Plants low, 8–16 cm	Plants intermediate, 18–38 cm	Plants tall, 15–90 cm
Plants not woody above ground	Plants woody at base, or only a little above	Plants woody well above ground
Leaves congested near base of plant, the lower internodes much shorter than the leaves (internode/leaf index 0.2–*0.5*–1.0), the upper internodes much longer (index 1.1–*2.5*–5.2).	Intermediate: lower internodes, index 0.7–*1.3*–2.0; upper internodes, index 1.9–*2.6*–4.3.	Internodes about equal; lower internodes, index 1.0–*1.8*–2.7; upper internodes, index 1.3–*1.9*–3.3.
Second index/first index = 5	Second index/first index = 2	Second index/first index = 1+
Secretory cells subapical and scattered	Secretory cells subapical	Secretory cells mostly subapical
Flowers and fruits few	Flowers and fruits intermediate, never abundant	Flowers and fruits abundant
Corollas campanulate, the lobes not usually spreading	Corollas usually broadly flaring-campanulate	Corollas rotate
Pedicels 1–4 times as long as fruits	Pedicels 1–3 times as long as fruits	Pedicels shorter than fruits
Ovary hairs short, falcate, ascending	Ovary hairs intermediate in length, erect or spreading, straight or falcate	Ovary hairs long, straight, spreading
Altitudinal range: Los Angeles Co., 6400–7800 ft.; San Bernardino Co., 7000–7700 ft.	Altitudinal range: Los Angeles Co., 5320–7300 ft.; San Bernardino Co., 5000–7000 ft.	Altitudinal range: Los Angeles Co., 1000–5600 ft.; San Bernardino Co., 1500–7600 ft.

Galium angustifolium Nutt. ex Torr. & Gray. Plants growing tall by means of slender woody scaffold stems, or low and tufted from a woody base; internodes subequal; inflorescences diffuse and many-flowered, or sometimes few-flowered, the pedicels on pistillate plants usually much shorter than ovaries; secretory cells usually subapical, but sometimes scattered; corollas rotate; ovaries and fruits appearing round, the hairs usually abundant and as long as the diameter of the fruit.

Hilly and mountainous areas, in places where roots are sheltered from heat and drought. From Sierra San Pedro Mártir, Baja California, north to the Santa Lucia and Gabilan ranges of Monterey and San Benito counties; eastward in Kern Co. to the west slopes of the Sierra Nevada, and in San Bernardino Co. to the Providence Mountains.

GALIUM ANGUSTIFOLIUM Nutt. ex Torr. & Gray, Fl. N. Amer. 2:22. 1841, ssp. ANGUSTIFOLIUM, as a synonym, Bot. Calif. 1:285. 1876. Type from "San Francisco? *Douglas!*", the locality certainly erroneous. *G. trichocarpum* Nutt., l. c., type from "St. Diego," *Nuttall* (PHIL). Not *G. trichocarpum* DC. *G. siccatum* Wight, Zoe 5:54. 1900. Type from Del Mar, San Diego Co., *T. Brandegee* (CAS). *G. angustifolium* var. *siccatum* (Wight) Hilend & Howell, Leafl. W. Bot. 1:135. 1934. *G. angustifolium* var. *bernardinum* Hilend & Howell op. cit. 134. Type from near Cactus Flats, San Bernardino Mountains, *Hilend 475* (CAS). *G. angustifolium* var. *diffusum* Hilend & Howell l. c. in part. Type from Saragosa Springs, upper Holcomb Valley, San Bernardino Mountains, *Hilend 533* (CAS). *G. angustifolium* var. *typicum* Hilend & Howell op. cit. 154. 1935.

Plants (15) 30–60 (100) cm high, the fertile branches arising singly or in tufts from the nodes of slender, woody, erect or arching scaffold stems (fig. 4D) or less commonly tufted from near the ground; stems glabrous to hispid, the internodes commonly 2–7 cm long, generally much longer than the leaves, at least on scaffold stems; leaves glabrous to canescent, 5–27 mm long, filiform to strap-shaped, tapered or abruptly acute at apex, the margins usually set with hairs of several sizes pointed in different directions; inflorescences usually profuse, but sometimes reduced, the flowers and fruits usually very abundant; corollas cream colored to greenish yellow, never conspicuously more hispid than the leaves and stems; **2n = 22, 44.**

Cliffs, canyons, and hillsides, in protection of trees, shrubs, or rocks, at 50 to 8200 feet; granite, shale, or sandstone. Sierra San Pedro Mártir, and northward in the Coast Ranges to Monterey and San Benito counties; Tehachapi and Greenhorn Mountains; Santa Catalina Island.

After subtraction of seven subspecies, what remains to ssp. *angustifolium* is still complex. The diploid form is the only form in Baja California and southern San Diego Co. Thence, northward through Riverside and southwestern San Bernardino counties, it is interfingered and interspersed with tetraploid forms. From Orange Co. northward into Monterey and San Benito counties, and in central Kern Co., apparently all of the populations are tetraploid.

The diploid form is readily defined: plants fairly tall, stems and corollas glabrous or nearly so, leaves only sparsely hairy and of small to moderate size. The tetraploids, on the other hand, are variable, being very tall or quite low and compact, glabrous or canescent on stems, leaves and corollas, and the leaves are sometimes considerably larger than in the diploids. All canescent plants are tetraploid, but most tetraploid plants are not canescent. Many tetraploids are recognizable by oversized leaves and flowers, but most of them do not exhibit this quality. Many tetraploid individuals are, in fact, indistinguishable from diploids, and it is

therefore impractical to separate the two races taxonomically, especially in consideration of their overlapping ranges.

Subspecies *angustifolium* remains, therefore, highly variable, particularly as to the included tetraploids. Among the latter can occasionally be recognized something of the low compact habit and narrow inflorescence of ssp. *nudicaule,* as for instance in San Diego Co., *Bacigalupi 3915,* suggesting introgression from that subspecies. The possibility of introgression from ssp. *foliosum* in Ventura Co. is discussed below under that subspecies. The canescence of much of the tetraploid material has no counterpart in any known diploid, a situation apparently homologous with that in *G. bolanderi* Gray, of the fleshy-fruited group.

The following names were reduced to synonymy for the reasons given: *G. siccatum* Wight, although striking in appearance, cannot be maintained as a separate taxon, because the canescent character which distinguishes it occurs sporadically throughout the tetraploid portion of the range, and because even at the type locality we find the population variable with regard to this character (*4347*). Variety *diffusum* Hilend & Howell comes close to our ssp. *gracillimum,* under which see discussion. Variety *bernardinum* Hilend & Howell is a rather low compact form without geographic unity, being based on quantitative characterse which appear here and there throughout the range.

Galium angustifolium Nutt. ex Torr. & Gray ssp. **borregoense** Dempster & Stebbins, ssp. nov. A ssp. gracillimi simile, sed corollis hispidis, caulium angulis crassis (latera simulantibus), cellulis secretoriis subapicalibus discedit.

Type from Palm Canyon, Borrego Valley, San Diego Co., California, *Munz & Hitchcock 11,339* (POM 172789).

Similar to ssp. *gracillimum,* but corollas hispid with long hairs, leaves larger, more glabrous, and apparently not fugacious, the stem angles greatly expanded, presenting more surface than the sides except in older stems (fig. 5J); secretory cells mostly subapical; presumably diploid (stomata 33μ).

Only two collections are known: *4375* (staminate) and the type (pistillate), both from lower Palm Canyon, San Diego Co., where it is rare. The number of morphological differences, together with its isolated locality, south of the Santa Rosa Mountains in the Colorado Desert, dictate its separation from ssp. *gracillimum* of the Mohave Desert. Plants of the Palm Springs area, Riverside Co., lie between the two localities, i.e., south of the Little San Bernardino Mountains, but north of the Santa Rosa-San Jacinto mountain barrier, and although their location in the Colorado Desert rather than the Mohave suggests their inclusion with ssp. *borregoense,* they belong morphologically with ssp. *gracillimum.* Of the 5 collections from the Palm Springs area, one (*Spencer 1476,* POM), however, has hispid corollas, but its stems lack the exaggerated angle development found in ssp. *borregoense.*

GALIUM ANGUSTIFOLIUM Nutt. ex Torr. & Gray ssp. **foliosum** (Hilend & Howell) Dempster & Stebbins, comb. nov. *G. angustifolium* var. *foliosum* Hilend & Howell, Leafl. W. Bot. 1:134. 1934. Type from Anacapa Island, *Howell 3792* (CAS).

Generally congested subshrubs (fig. 4E) 30–60 cm high, the internodes commonly 2–15 mm long, but those on scaffold stems occasionally longer (to 55 mm); the closely set nodes prominent after leaf-fall; stems glabrous, the angles much thickened, often nearly obscuring the faces in slender upper stems (fig. 5K); leaves narrowly linear, 3–11(17) mm long, often longer than internodes, nearly glabrous on the surfaces, the margins smooth, with few stout regularly spaced subequal apically directed hairs; flowers and fruits small, abundant, congested in complex amorphous inflorescences; corollas glabrous or obscurely hispid; **2n = 22.**

Exposed rocky slopes, 100 to 200 feet. Santa Cruz, Santa Rosa, and Anacapa Islands. Doubtfully on the mainland in Ventura Co. (see below).

This subspecies, like *G. californicum* H. & A. ssp. *miguelense* (Greene) Dempster & Stebbins, may derive its congested character in part directly from the windy island habitat. However, both the congested sub-shrubby habit and the small slender leaves are pretty consistent in *G. angustifolium* of the northern group of Channel Islands, in sharp contrast to *G. angustifolium* of the southern group, and it seems extremely likely, therefore, that they are genetically determined. Moreover, we have seen the plants growing in fairly sheltered places on Santa Cruz Island without diminution of these characters, and material transplanted to Contra Costa Co. remained in character *(4083)*.

Several collections from the Ventura Co. mainland resemble ssp. *foliosum* in varying degrees. It may be that true ssp. *foliosum* does occur there, but careful examination of the specimens casts much doubt upon this supposition. Subspecies *foliosum* is diploid, at least on Santa Cruz Island, and the cytologically known collections of ssp. *angustifolium* northwestward from San Bernardino Co. are tetraploid. Mainland material resembling ssp. *foliosum* is, however, of unknown chromosome number, and measurement of stomata gave no clue, since the overlap in size of stomata of diploids and tetraploids is too great (ssp. *foliosum* 32–*38*–41μ; tetraploid ssp. *angustifolium* 34–*40*–48μ). Study of marginal leaf-hairs seems significant, however, since in this respect the island material is rather uniform: the hairs, unlike those on mainland material, are of uniform size, evenly spaced, and rather stout for their length, the leaf margins being otherwise smooth. Mainland material has marginal hairs of several sizes, irregularly interspersed, and they are relatively slender. One collection allegedly from the mainland does indeed include material that appears to be ssp. *foliosum*. This is a sheet of four specimens, two apparently ssp. *foliosum* and two resembling the mainland forms, collected by T. S. Brandegee allegedly at Ventura in July, 1885 (CAS). The handwriting on the label appears to be that of Alice East-

wood rather than T. S. Brandegee, and there is a possibility that the two specimens of ssp. *foliosum* in fact came from Santa Cruz Island. It must be remarked, however, that since plants resembling ssp. *foliosum* are found only in Ventura Co., they may well be indicative of introgression from island material, either by way of seed or pollen transportation.

GALIUM ANGUSTIFOLIUM Nutt. ex Torr. & Gray ssp. **gabrielense** (Munz & Johnston) Dempster & Stebbins, comb. nov. *G. gabrielense* Munz & Johnston, Bull. Torrey Club 51:299. 1924. Type from ridge east of Ontario Peak, San Bernardino Co., *Munz 6078* (POM). *G. siccatum* var. *anotinum* Jepson, Manual Fl. Pl. Calif. 962. 1925. Type from Mt. San Antonio, *Peirson 215* (JEPS).

Plants usually low, 6–20 (36) cm high, tufted from a woody base; stems hispid, the internodes a little shorter than to twice as long as the leaves; inflorescences narrow, relatively few-flowered, the branchlets short, ascending, little compounded; leaves 2–14 mm long, linear to sometimes oblong or elliptical, more or less hispid with short, rather stout hairs, the apex more or less acute; corollas yellowish or often red, hispid externally with few to many bristles, longer than those on stems and leaves; fruit body about 1½–2 mm long, the pedicel ¼–1½ times as long, the hairs luxuriant, about as long as fruit body or longer; **2n = 44.**

Dry rocky or sandy granite slopes and ridges, in open forest or high chaparral, at 4000 to 8700 feet. Vicinity of San Antonio Canyon, Los Angeles and San Bernardino counties; upper San Gabriel Canyon, Los Angeles Co.

Aside from being tetraploid and hairy-stemmed, much of the material of ssp. *gabrielense* differs little from ssp. *nudicaule* (table 4; fig. 11). As might be predicted, however, the tetraploid subspecies is much more variable. Nevertheless, the plants do not usually exceed 20 cm in height, the leaves and stems are usually very hairy, and the hispid corollas, as with ssp. *nudicaule,* are diagnostic. Subspecies *angustifolium* as found in the wash near Claremont at the mouth of San Antonio Canyon presents a marked contrast, being much taller, with glabrous stems and corollas and profuse inflorescence. There is, however, some evidence of introgression, at least from ssp. *angustifolium* into ssp. *gabrielense,* and intermediates can be cited, e.g. *4295* (4x), *Hardham 14,288* (JEPS), *Johnston s.n.* from Cascade Canyon (POM).

GALIUM ANGUSTIFOLIUM Nutt. ex Torr. & Gray ssp. **gracillimum** Dempster & Stebbins, ssp. nov. *G. angustifolium* var. *diffusum* Hilend & Howell, Leafl. W. Bot. 1:134. 1934, in large part, but not as to type.

Caules glabri; inflorescentiae laxae; folia gracilia saepe ephemera; flores fructusque parvuli; cellulae secretoriae in ordinibus duobus dispositae.

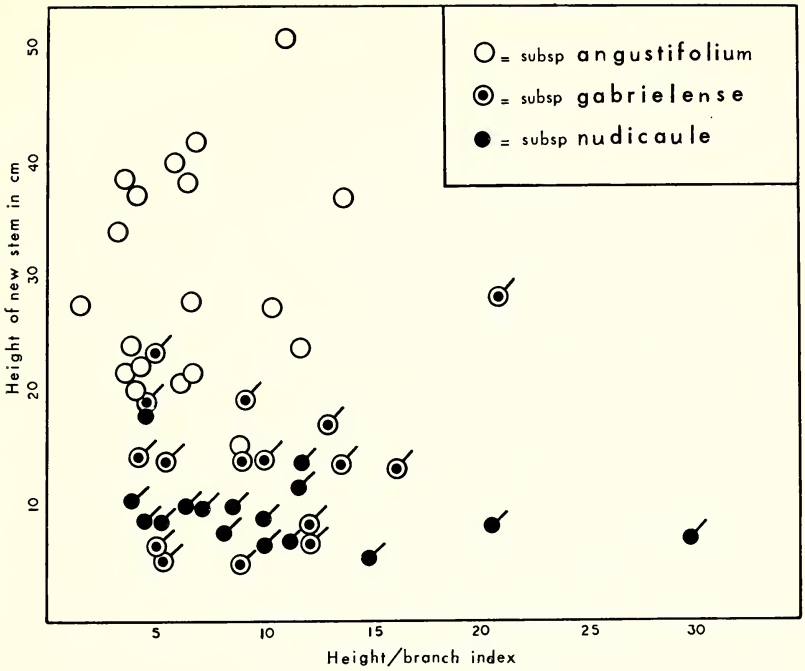

FIG. 11. Scatter diagram to show intermediacy of ssp. *gabrielense* between ssp. *nudicaule* and ssp. *angustifolium* of the same general area. Height/branch index was obtained by dividing length of shoot by the length of the longest branch of the inflorescence. Height in this instance refers only to current year's herbaceous growth. Oblique line indicates hispid corollas.

Type from Black Rock near Warren's Well, Little San Bernardino Mountains, San Bernardino Co., *Epling & Robison s.n.,* June 25, 1933 (DS, RSA, UC 574879-holotype).

Plants very slender throughout (fig. 4F), commonly 40 cm long from the persistent woody stems; stems glabrous, the internodes commonly 2 to 3 times as long as leaves; leaves small, 4–15(18) mm long, very narrowly linear to slightly oblanceolate, scabrous, somewhat ephemeral; secretory cells usually in two longitudinal bands each side of the midrib (fig. 7J); inflorescence very openly paniculate, the flowers and fruits rather abundant but very small; pedicels usually shorter than (to 3 times as long as) ovaries, but branchlets long and flowers thus not congested; corollas generally glabrous, but rarely hispid, about 1½–2 mm across, yellowish or tinged with pink; fruits less than 2 mm long, the hairs ½–¾ as long; **2n = 22.**

Among granite rocks and boulders in partially shaded places in canyons and at northern base of rocky outcrops, 400 to 4800 feet. Providence and Little San Bernardino Mountains and east side of San Jacinto Mountains, San Bernardino and Riverside counties.

Table 4. Some Comparative Characters of Three Subspecies of Galium angustifolium

Subspecies *nudicaule* is represented by 20 individuals from Cloudburst Summit *(4123, 4236)* in the San Gabriel Mts; ssp. *gabrielense* is represented by 18, including all suitable plants from all pertinent collections; and ssp. *angustifolium* is represented by 19 from known or suspected diploid collections, chiefly from Swartout Valley and the San Bernardino Mts. In most of the characters measured, ssp. *gabrielense* is closer to ssp. *nudicaule* than to ssp. *angustifolium,* despite the deliberate inclusion of aberrant individuals from peripheral areas, suspected of introgression from ssp. *angustifolium*. For explanation of internode index and branch index see legends for Figs. 10 and 11, respectively.

	nudicaule	*gabrielense*	*angustifolium*
Height of new wood in cm	6–*9.3*–19	5–*11.8*–19.5	15–*31*–54
Leaf length in cm	0.3–*0.5*–1	0.4–*0.8*–1.4	0.8–*1.1*–1.6
Internode index	2.1–*4.6*–6.7	*2*–*4*–7	5.1–*7.7*–14.3
Branch index	*2*–*3.6*–7.4	1.3–*3.4*–6.6	1.6–*3.3*–5.8
Height/longest branch	4–*10*–30	4.3–*9.1*–21.5	*2.2*–*6.5*–14.6
Corollas	All hispid	All hispid	18 glabrous 1 pubescent
Stems	All papillose	15 hispid 3 glabrous	All glabrous

This diploid and definitely deserticolous subspecies is readily recognized by its slender open habit and strikingly small leaves, flowers, and fruits. All of these diagnostic characters remained unchanged from one winter to another under cultivation in Contra Costa Co. where, however, the plants did not survive the second winter.

The relationship of ssp. *gracillimum* to var. *diffusum* Hilend & Howell must be considered. Hilend & Howell (1935) included in their variety all of ssp. *gracillimum* and a great deal besides, being guided apparently by similarity in the habit and general appearance of the plants. We prefer, however, to limit ssp. *gracillimum* to plants of the oases and granite outcroppings in the true desert. The type of var. *diffusum* (Saragosa Spring, Holcomb Valley, San Bernardino Mountains, *Hilend 533,* CAS) can unfortunately not be included. Although it nearly resembles our desert plant, the flowers and leaves are slightly larger, and the latter are not caducous. Furthermore, the habitat is completely different, namely forested terrain in the San Bernardino Mountains at 7500 feet altitude. We therefore refer it to ssp. *angustifolium.*

Galium angustifolium Nutt. ex Torr. & Gray ssp. **jacinticum** Dempster & Stebbins, ssp. nov. Altitudine plantae totae moderata (17–35 cm), foliis magnis (11–26 mm), inflorescentiis parvis, corollis plerumque hispidis.

Type from Black Mountain road, 0.9 mile above junction of road to

Table 5. Some Comparative Characters of Three Subspecies of Galium angustifolium

	nudicaule	*jacinticum*	*angustifolium**
Length of shoot of current year in cm	6–*9.3*–19	12.5–*18.4*–25.5	16.5–*32.5*–45
Length of leaf in cm	0.3–*0.5*–1	1.4–*1.7*–2.7	0.6–*1*–2
Corollas	20 hispid	13 hispid 8 sparingly hispid 1 glabrous	19 glabrous

*From the San Jacinto Mountains. If the plants had been measured from the ground, including the woody stems, the result would have been a great increase in the first figure for ssp. *angustifolium,* and almost no changes in the corresponding figure for the other two subspecies.

Pine Wood, San Jacinto Mountains, Riverside Co., *Dempster & Stebbins 4244* (JEPS-54620).

Plants moderately low, commonly 17–35 cm, the leaves relatively large; stems glabrous, the internodes about as long as the leaves; leaves 11–26 mm long, strap-shaped, abruptly narrowed at apex, glabrous or very shortly hairy on the surfaces, the apically directed marginal hairs longer; inflorescences relatively simple, narrow and few-flowered; corollas usually hispid, the hairs much longer than those on the leaves. **2n = 66.**

In partial shade in open mixed forest, 4200 to 6500 feet. West side of the San Jacinto Mountains.

This narrow endemic, found only in the Lake Fulmor-Black Mountain area of the San Jacinto Mountains is, however, not uncommon there. It is readily distinguished from diploid ssp. *angustifolium* of the same general area by its almost invariably hispid corollas, its relatively low habit, large leaves, and sparse inflorescences. The tetraploid plants of the northern San Jacinto Mountains, although the majority (5:2) have some bristles on their corollas, and the leaves tend to be large, are unlike ssp. *jacinticum* in being tall and woody. Tetraploids of the Santa Rosa Mountains to the south also have mostly somewhat hispid or pubescent corollas and are, in addition, low and largely lacking woody stems. They differ from ssp. *jacinticum,* however, in their consitently small leaves.

The hispid corollas, low non-woody habit, and sparse inflorescences, all suggest ssp. *nudicaule* as one of the progenitors of both ssp. *jacinticum* (table 5) and the tetraploids of these mountains, which are, however, tall. We are unable to account for the large leaves of ssp. *jacinticum* except to note that large leaves are often associated with polyploidy, as for instance in the tetraploids of central San Diego Co. and elsewhere, and in hexaploid *G. johnstonii.*

Representative collections. Riverside Co., San Jacinto Mountains: Fulmor Lake, *4129;* Alandale Pines, *4130;* Black Mountain Road, *4246.*

GALIUM ANGUSTIFOLIUM Nutt. ex Torr. & Gray ssp. **nudicaule** Dempster & Stebbins, ssp. nov. A ssp. gabrielensi simile sed foliorum pilis brevioribus, caulibus papillosis omnino glabris differt.

Type from Cloudburst Summit, Angeles Crest Highway, Los Angeles Co., at 7020 feet, *Dempster & Stebbins 4236* (JEPS-54621).

Plants low, 6–16 cm high (fig. 4C); stems glabrous, more or less papillose, the internodes a little shorter than to twice as long as leaves; leaves 2–10(15) mm long, linear, or the shortest sometimes oblong or elliptical, more or less hispid with short hairs, the apex more or less acute; inflorescences narrow, relatively few-flowered, the branchlets short, ascending, little compounded; corollas usually red, often very dark but sometimes yellow, hispid externally with few to many slender bristles, which are longer than those on the leaves; fruit body about 1½–2 mm long, the pedicel ¼–1½ times as long, the hairs luxuriant, about as long as fruit body or longer; **2n = 22.**

Steep sandy east- and south-facing slopes, in very open mixed forest; granite soil. Central San Gabriel and eastern San Bernardino mountains, at 6700 to 8200 feet.

The two well-separated populations of the central San Gabriel Mountains and the eastern San Bernardinos respectively have diverged somewhat in their evolution, but scarcely enough to merit separate names. Plants from the San Bernardino Mountains are considerably less hairy on corollas, leaves, and ovaries, the stems a little more elongated and scarcely papillose. There is no indication that the San Gabriel plants hybridize with either *G. jepsonii* on the same ploidy level (although they grow very near together at Cloudburst Summit, for instance) or with ssp. *angustifolium,* which in Los Angeles Co. seems to be all tetraploid. In the San Bernardino Mountains, however, where diploid ssp. *angustifolium* occurs, it is possible that introgression from that source may account for the fewer hairs, slightly greater stem elongation, and more apically directed leaf hairs or ssp. *nudicaule.* There is some evidence also of introgression in the other direction, or of hybridization with chromosome doubling, since two of our tetraploid collections of ssp. *angustifolium* from the San Bernardino Mountains (*4152* and *4154*) include plants with truly hispid corollas.

Representative collections. Los Angeles Co., San Gabriel Mountains: Mt. Waterman, *Ewan 10,028* (CAS, NO); Mt. Islip, *Fosberg & Ewan 4915* (NO). San Bernardino Co., San Bernardino Mountains: Cienega Seca Creek, *4147, 4150.*

GALIUM ANGUSTIFOLIUM Nutt. ex Torr. & Gray ssp. **onycense** Dempster & Stebbins, comb. nov. *G. angustifolium* var. *onycense* Dempster, Brittonia 10:189. 1958. Type from hill above Onyx Ranch, near Onyx, Kern Co., *Dempster, Bacigalupi, & Robbins 1015A* (JEPS).

Plants grayish-green, slender, 12–30 (commonly 15–18) cm tall from the woody base; stems scabridulous or very shortly hispid, the hairs few,

very short and spreading; angles of stems very broad, often largely concealing the true faces (fig. 5F); internodes 2–2½ times as long as leaves, or a little longer in the inflorescence; leaves commonly 5–10(14) mm long, lanceolate, tapered gradually to an acute apex, the lower surface commonly glabrous, the upper surface and margins sparsely short-bristly, the hairs somewhat apically directed; inflorescence not narrow, the branchlets somewhat elongated; corollas hispid, usually pink; ovary and fruit hairs luxurious, longer than fruit body; **2n = 22.**

Growing from under and between large granite rocks and outcrops, with scattered Digger Pine and oaks, not common. Between Fay Creek and the crest of the Sierra Nevada in northern Kern Co., 3000 to 7200 feet.

This diploid subspecies is closest to ssp. *nudicaule,* but the plants are more lax, the inflorescences fuller and more open, the stems scabridulous, the leaves more acute and less hairy. It appears to have diverged in its evolution as a result of isolation and of selection for a more rigorous summer climate.

Representative collections. Kern Co.: Fay Creek, *Howell & True 41,811* (CAS, JEPS); near Onyx, *Voegelin 147, 131* (both UC), Dempster, Bacigalupi, & Robbins 1015B (JEPS); Spanish Needle Creek, *Twisselmann 10,911, 10,923, 10,924, 12,153* (all CAS, JEPS); west of Walker Pass, *1431.*

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